Early Scotopic Dark Adaptation

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ABSTRACT OF DISSERTATION

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Abstract

The human visual system can function over a broad range of light levels, from few photons to bright sunshine. I am interested in sensitivity regulation of the rod pathway in dim light, below the level at which the cones become effective. I obtained thresholds for large (1.3 deg) and tiny (5 min arc) circular test spots, either after 20-30 mins exposure to complete darkness (absolute threshold), or on uniform backgrounds of varying light intensities, or just after the background was removed to plunge the eye into darkness; Maxwellian view optics were used so that variations in pupil size would have no effect. The overall theory is that sensitivity in the rod system is adjusted by a slow process of adaptation in the retina driven by the long-term mean background light level and a rapid process sensitive to variability in the light provided by the background (“photon noise”). My data show that thresholds for tiny test spots primarily reveal the photon-driven noise effect, and those for large test spots reveal both processes. The traditional idea that all components of rod dark adaptation are slow is challenged here, since almost immediately after the background light is removed, thresholds of tiny spots drop to absolute threshold directly, and thresholds of large test spots drop half-way to absolute threshold before continuing to recover back to absolute threshold over the next 25 minutes. These initial rapid drops in threshold are accounted for by the postulated photon-variability-driven rapid process, as removing the background removes the noise.
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I would like to dedicate this work to my grandma and PapPap Mary and Harry Denham. My thoughts are with you everyday even though I cannot be. It is from you that I learned what real dedication means.
In Chapters 1 and 2 I will discuss the background research regarding light and dark adaptation, highlighting both psychophysical and physiological data. Specifically, I will dissect the classic rod TVI curve and discuss each segment in detail. In Chapter 3 I will summarize some literature regarding the mechanism regulating scotopic sensitivity. Specifically, it is largely believed that scotopic sensitivity is limited by dark light and neural adaptation. I hypothesize a scotopic sensitivity regulating mechanism containing a rapid process driven by photon noise from the light source, and a slow process of adaptation driven by the long-term mean background light level. The fourth chapter will describe the general methods used in the current research. In Chapter 5, I will measure rod increment thresholds on steady backgrounds with large (1.3 deg) and small (5’ arc) test spots, which should replicate the well-known Weber and Square Root Laws, respectively. I will also measure thresholds for both test sizes immediately after turning off the background, to test the hypothesis that the consequent removal of photon noise due to the background ("photon-noise abolition") is responsible for the resulting drop in test threshold. I expect thresholds to drop from the square root TVI curve immediately to absolute threshold in the case of the 5’ arc test, and from the Weberian TVI curve to the Square-Root Law in the case of the 1.3 deg test. A further consideration is the delay time from background offset to test presentation; this delay should have no effect on threshold if photon-noise abolition is the only factor involved. I tested several delays to determine if this was the case or not, which will be discussed in Chapter 6. All delays were equal to or longer than the integration time of the scotopic pathway. The seventh chapter will discuss data in which the background display and a test stimulus were flashed simultaneously without allowing
observers to light adapt between trials in the first condition (the interval between flashes
being dark). The second condition will present the test spot immediately after a briefly
flashed background. I hypothesize that photon noise in the background added to the test
spot will cause a decrease in sensitivity (simultaneous flash condition), but the briefly
flashed background preceding the test spot will have no effect on sensitivity which will
remain at the level found after long-term dark adaptation. Finally, in Chapter 8 I will
discuss the results of all experiments, elaborating specifically on what can be learned about
the rod system and scotopic sensitivity regulation from this research.
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Chapter 1: Light Adaptation

The human visual system can perceive wavelengths from about 400-700 nanometers and respond to luminance intensities that cover over 10 log units. Reflected light from the environment enters the eye through the pupil and is focused into a sharp image by the cornea and lens. Focused images are then transformed into electrical signals in the visual receptors of the retina, the rods and cones. The rods are responsible for vision in dark and dimly lit conditions, while the cones are responsible for vision in brighter luminance conditions.

Initially, the visual system of primates was only made up of cones allowing these animals to see in environments with higher ambient lighting (Land & Nilsson, 2002). With the later evolution of rods, primates gained the ability to see not only in the light, but also at night when very few photons are present. The main objective of the rod system is to be able to detect weak light sources (reflective surfaces seen in starlight), including single photon detection. This objective varies vastly from that of the cones that function to detect changes in contrast. Additionally, with only one class of rods, the scotopic system does not have the ability to detect color, unlike the cones that allow us to perceive color based on the ratios of inputs from the three cone classes (L, M, S).

Adaptation, the ability to maintain vision over a wide range of light intensities, is in part due to the constriction of the pupil and the shift from rod- to cone-mediated vision and vice versa. The current research seeks to understand the process of adaptation in the rod system. I will control for pupil size variations using Maxwellian view optics and will work at light levels that are too low to influence the cones. Adaptation occurs constantly, as the lighting in our environment is continuously changing. Light adaptation happens rapidly,
while dark adaptation, an increase of sensitivity that occurs as the eyes stay in the dark, typically occurs more slowly.

Light adaptation can be studied using increment thresholds (Stiles, 1939). In these experiments, a target stimulus is presented in the parafoveal region on a background of certain luminance intensity (Figure 1.1). Cones are most concentrated in the fovea, although there are some present in the peripheral region of the retina. The rods outnumber the cones in the parafovea and periphery of the retina; thus eccentric fixation can be used to preferentially stimulate rod vision. Target flashes are set to threshold to probe the state of adaptation set by the continuously-presented background. As the target is brief, weak, and small, it is assumed not to affect the state of adaptation. The background luminance intensity is adjusted incrementally, from very dim to very bright. The observer adapts and measures his or her threshold at each new light level, allowing experimenters to obtain the entire range of rod thresholds, from absolute threshold in the dark to when the cones take over on brighter backgrounds. Thresholds are determined when the target intensity is adjusted to the lowest level at which the observer can still distinguish the target from the background.
Figure 1.1. Example of experimental stimuli used for TVI experiments. This schematic depicts the current experimental stimuli. The portion labeled I refers to the adapting background with intensity (I). The test spot (T) is presented with the background to measure varying thresholds based on the amount of ambient light present. The four green dots in the center indicate attentional aids. The green dot at the bottom of the circle indicates the observer’s fixation location.

Threshold increment curves (threshold versus intensity or TVI curves) for large spots have been used to characterize the properties of light adaptation (Figure 1.2). TVI curves, as the name suggests, plot threshold increments as a function of background intensity (in log units due to the large range of human vision). The term “increment” is used when the target is added to the background. The “threshold increment” is the target intensity, ΔI or T, excluding the background on which it falls (I). The observer views I when the target is absent and I + ΔI when it is present. The classic Aguilar and Stiles (1954) curve, using rod isolating conditions and obtained with large test spots, is customarily divided into 4 segments, such that dark light and photon noise determine the first two
segments (flat and square root), and Weber-law processing and saturation determine the upper two segments (Wyszecki & Stiles, 1982).

All four regions will be briefly summarized, and then segments 1-3 will be explained in more detail, devoting a brief section of text to each; understanding these regions is critical to the logic of the current research. In this thesis, a contribution of photon noise to the Weber law segment will be hypothesized.
**Classic TVI Summary**

The left-hand asymptote of the classic curve, corresponding to very dim or zero background levels, is referred to as “dark light”. Dark light is due to internal noise in the retina from thermal isomerizations of the photopigment, spontaneous opening of photoreceptor membrane channels, and spontaneous neurotransmitter release (Baylor et al., 1984; Baylor, 1987). Dark light sets the absolute threshold and the flat portion of the TVI curve, when the background (or the field) is so dim that its effect on threshold is masked by the stronger dark light.

The second portion of the TVI curve, where the threshold begins to increase, follows the Square Root Law or de Vries-Rose law (Rose, 1942, 1948; de Vries, 1943). When the background light level has increased, its properties begin to affect threshold. The increase in threshold at this portion of the curve, if limited by quantal fluctuations in the background, should be proportional to the square root of the background luminance, which is approximately a slope of 0.5 on a log-log plot.

The third portion of the curve for large spots approaches Weber’s Law. Weber’s Law is defined as $k=\Delta I/I$, where $k$ is a constant, $\Delta I$ is the increment threshold on the background $I$ ($\Delta I$ is also referred to as the Just Noticeable Difference or JND; Weber, 1834, in Martin, 2000). This portion of the curve should have a slope of approximately 1 on a log-log plot, or exactly 1 if Weber’s law is precisely true.

The fourth portion of the TVI curve, referred to as “saturation” in figure1.2, indicates the point where the curve bends upward so that rods can only detect the stimulus if it is even brighter than predicted by Weber’s Law. Above saturation, the cones detect the stimulus (not shown). The switch from scotopic to photopic vision depends not only on test
and background intensity but also on test and field wavelength, test size, test duration, and test eccentricity.

Barring saturation, the entire TVI cure can be modeled by Fechner’s improvement to Weber’s law (Fechner, 1860), namely to include a term for noise, \( I_0 \), necessary to avoid an infinite threshold at zero intensity (total darkness or \( I=0 \)). Fechner’s improved equation is \( \Delta I/(I+I_0) = k \). Figure 1.2 is the graphical depiction of this equation.

**Absolute Threshold**

Absolute threshold is the minimum amount of energy needed to detect a test stimulus in total darkness, i.e. in the absence of a background, after long-term dark adaptation has occurred. At absolute threshold, \( I=0 \) and \( \Delta I = k I_0 \). At this point the rods are functioning in true isolation and visibility is limited by noise in the stimulus and the photoreceptors. When measuring absolute threshold psychophysically, it is apparent that this value depends on both the size and duration of the test flash (Hecht, Shlaer, & Pirenne, 1942) since these manipulations will alter the number of quanta caught by the rods and thus the number of rhodopsin molecules photoisomerized. Some quanta incident at the cornea excite the rods; the rest are lost in the ocular media, absorbed by the cones, pass the rod pigments undetected, or are degraded into heat. Using various correction values (see Sharpe 1990 for a detailed breakdown), it can be estimated that approximately 20% of the quanta incident at the cornea excite the rods (for 505nm lights). Classic values reported by Hecht et al. (1942) suggest that using small (10 min), brief (1-10 ms) test flashes produces the smallest energy threshold necessary to detect the target. The exact number of absorptions that allows detection varies from trial to trial due to the internal noise of the
visual system and photon fluctuations. Spontaneous firings of visual neurons can cause enough noise to prevent the system from detecting the test flash. Thus, the actual visual signal must be greater than the internal noise for observers to be able to detect a dim light reliably. Hecht et al. (1942) suggest 5-14 absorptions are sufficient for detection. Sakitt (1972) showed that even fewer are needed for detection. With so few quanta, the chance that any particular rod receives more than 1 quanta is minute. Therefore, single quantal catches in no more than 5-14 rods support vision in total darkness.

When a dim background is added to the test flash, the threshold curve does not rise at first, but stays at absolute threshold. This portion of the curve, labeled dark light in Figure 1.2, can be attributed to internal properties of the phototransduction process. Internal properties include retinal noise, which can arise from the opening and closing of channels in the outer segment of the photoreceptor (Lamb, 1987), biochemical intermediate variability, and the spontaneous thermal activation of the rhodopsin molecule (Baylor et al., 1984), as well as the reversibility of the all-trans conversion following bleaching by intense lights (Lamb, 1987). Noise created in higher cortical areas may also be involved in limiting absolute threshold. Central sources of noise are thought to include (at least) the random release of neurotransmitters, variations in the thresholds necessary for spiking, and fluctuations in the observer’s criterion.

**Dark Light**

As noted above, when very dim light is added to the background, the threshold remains constant and at absolute threshold (the so-called ‘foot’ of the TVI curve). This can be accounted for by ‘dark light.’ The term dark light has been used to describe this limit on
absolute threshold, as it can be thought of as a dark or imaginary light causing activity in
the photoreceptors, activity that the test flash must overcome to be visible; Fechner used
the term “intrinsic light” for this, and thought of it as a fixed level. When the background
light is very dim, it adds little to the dark light and so the latter controls threshold. The
precise psychophysical measurement of dark light is unknown, but it can be quantified
with an ‘equivalent’ real light, estimated from the low end of the threshold increment
curve, and is defined as the value where the constant slope, or the Weberian portion,
intersects the absolute value measurement (Barlow, 1956; see Figure 1.2). A range of
0.111-0.013 scotopic trolands has been used as an estimate of the intensity of dark light for
an individual rod, which corresponds to a photopigment isomerization rate of 0.004-0.110
s\(^{-1}\) per rod (Barlow, 1957; Schneeweis & Schnapf, 2000). A psychophysical dark light
estimate for the standard human observer is roughly 1/1000 of this amount, although the
exact number is still debatable and depends largely upon estimates of temporal and spatial
summation for rod vision (Schneeweis & Schnapf, 2000). Dark light will be discussed
further in a detailed explanation of rod anatomy and phototransduction later in this
section. However, theories which attempt to generate psychophysical and physiological
estimates of dark light (such as those of Schneeweise and Schnapf, 2000) go beyond the
scope of this thesis. I will use only the psychophysical measurements.

**Quantal Fluctuations: Square Root Law**

As additional background light is added to a target stimulus, decreases in sensitivity
may be due to noise created by the external light source. The number of quanta available
for rod excitation from a steady lit background is not constant, but follows a Poisson
distribution. Rose (1942, 1948) and de Vries (1943) remarked that “the smallest possible threshold in a system that exhibits no intrinsic noise is set by the statistical fluctuations in the mean number of background photons entering the eye.” Put simply, the visual system must generate a signal from the increment test flash that is reliable enough to overcome the photon noise created by the background, plus any intrinsic variability. Rose and de Vries’ quantal fluctuation theory posits that incremental threshold measurements are proportional to the square root of the number of photons absorbed from the background. The second portion of the TVI curve shows this relationship between the increment threshold and adapting background intensity (Figure 1.2). Interestingly, rod thresholds collected with small test flashes follow the square-root law over a wider range than those collected using larger test spots (Barlow, 1956); the importance of this will be discussed later.

**Weber-Fechner fraction**

As the background intensity increases and the threshold increment curve begins to ascend beyond the region following the Square Root Law, these data are said to obey Weber’s Law, \( k = \frac{\Delta I}{I} \). For large test spots, the law holds over a four-log unit range, from 0.01 scotopic troland to about 100 scotopic trolands (See Fig 1.2). After the scotopic pathway receives enough excitation from the field (I) in addition to the dark noise (I₀), it begins to desensitize to the target and threshold levels increase. As the background level continues to rise, thresholds will be almost directly proportional to the background intensity; k is constant, so thresholds follow Weber’s law. The rate at which the slope changes from square root to Weberian is, again, dependent upon stimulus settings. In
contrast with absolute threshold, the Weber portion of the increment threshold curve is minimally related to intrinsic noise (internal retinal noise). At even higher adapting light levels, the rods will become “saturated” (Fechner’s equation no longer applies) so the cones will eventually begin to control target detection even if they have not yet taken over. Rod saturation occurs about two log units above the normal cone threshold. Rod saturation is only seen psychophysically when the Stiles-Crawford effect is used to increase the sensitivity of rods relative to that of cones (Aguilar & Stiles, 1954).

**Spatial & Temporal Summation**

Because the current experiments will utilize circular test spots on a background, it is important to note Ricco’s Law. This describes the relationship between the area of a target and the contrast necessary to be able to detect that target on a background. Ricco’s Law (Ricco, 1877) states that for foveal targets up to a certain diameter, threshold luminance should be inversely proportional to area, so that light intensity multiplied by the area of the test spot equals a constant at threshold. Thus, a larger test spot needs less intensity than a small spot to be detected. As the circular stimulus is moved further into the periphery, the stimulus diameter up to which Ricco’s law is valid increases from 42 min arc at 5 deg eccentricity to 1 deg at 20 deg eccentricity (Barlow, 1958).

Because the visual system must handle various rates of environmental change in luminance, it must have a mechanism to function under such conditions. There exists a critical duration for which the visual system can sum the amount of light entering the eye. The temporal integration period for the rods is up to about 100ms (Barlow, 1958), although this varies with the state of adaptation. Analogous to Ricco’s Law of spatial
summation, Bloch’s Law of temporal summation describes the relationship between the amount of time the test spot is displayed and the amount of light in the test spot necessary for detection (Bloch, 1885). Like Ricco’s Law, Bloch’s Law states that the stimulus duration multiplied by the light intensity equals a constant at threshold. Bloch’s Law holds true for stimuli whose durations are less than the period of temporal integration.
**Stimulus Parameters**

Threshold increment values are dependent upon the stimulus parameters; specific rod-isolation conditions must be used when collecting data from the scotopic system at high background intensities to avoid cone intrusion. Traditionally it was thought that light adaptation occurred strictly independently in the rods and cones. Some physiological and psychophysical evidence, however, contradicts this assumption (Sharpe, 1990), as the state of the cones has a small effect on the adaptation of the rods at bright background levels. In the following research, the upper ends of the TVI curves may not be entirely indicative of rod functioning. Specific rod isolation conditions will be discussed in Chapter 3: General Methods.
Chapter 2: Dark Adaptation

Dark adaptation refers to the recovery of visual sensitivity in the dark. The classic dark adaptation curve shows the change in sensitivity as a function of time spent in the dark (Figure 2.1). After pre-adapting to bright bleaching lights, observers exposed to complete darkness show a quick recovery of sensitivity within the first three minutes, then recover more slowly for the next 5-7 minutes (Lamb & Pugh, 2004). From about 11-40 minutes, sensitivity recovers even more slowly. After about forty minutes in the dark, visual sensitivity will no longer improve (absolute threshold). The top portion of the curve illustrates vision mediated by cones, or photopic vision. The bottom portion of the curve illustrates conditions under which the rods are functioning, or scotopic vision. Mesopic vision refers to the region between rod and cone vision in which both systems are responsive. When the rod pathway becomes more sensitive than the cone pathway, letting way for scotopic vision, colored test spots will appear achromatic to the visual system.
Figure 2.1. Taken from Widmaier, Raff, & Strang (2003). The classic dark adaptation curve showing the change in sensitivity as a function of time spent in the dark. Top portion of the curve indicates cone mediation, the second, shallower curve indicates rod mediation. Vertical axis: threshold, horizontal axis: time in dark. The bright light saturates the rods so they are much less sensitive than the cones for the first few minutes in the dark (the top portion of the rod adaptation curve) until they have recovered sufficiently to take over (the lower portion of the rod adaptation curve).

![Dark Adaptation Curve](image)

The length and slope of each branch of the curve is dependent upon the duration and intensity of the pre-adaptation bleaching period (Alpern, 1971). Longer and brighter pre-adapting periods cause a slower drop to absolute threshold. The size of the test spot also influences the shape of the dark adaptation curve. Small test spots are particularly good stimuli for cones, but not for rods. Taking advantage of the sizeable summation area of the rod pathway, larger test spots activate more rods permitting better sensitivity (Figure 2.2).
Dark adaptation curves are also affected by the wavelength of the test stimulus. As concluded by Graham, 1965, longer wavelength tests (reddish) produce about the same response in rods and cones, as both systems are about equally sensitive to long wavelength light. When short wavelength tests are used, however, rods are more sensitive than cones. Observers presented with a red test flash produce a monophasic dark adaptation curve, as the rod system can do no better than the cones since they have similar spectral sensitivities for long wavelength light. When observers are presented with a short wavelength light test (blue or violet), the curve looks biphasic. The cones are no longer more sensitive than the rods after the first few minutes when rods have part-way recovered; the rod branch of the curve will continue to drop until absolute threshold is reached.
Retinoid Cycle

When a photon of light hits the eye, it travels through the ocular media to reach the retina. Once reaching the retina, the photon may be absorbed by a photoreceptor. If absorbed, a cycle of biochemical reactions occurs to initiate vision. It is here, in the outer segment of the photoreceptors, that light is converted into electricity. The outer segments of the receptors have stacks of discs containing visual pigment molecules (rhodopsin). These visual pigment molecules go through a process of photoisomerization in which photoexcitation causes a structural change between isomers.

When light is captured by the 11-cis retinal chromophore (the part of the molecule responsible for the change in shape of rhodopsin), the chromophore is isomerized into its all-trans form (Lamb & Pugh, 2004). After this photoisomerization, rhodospin is converted into metarhodopsin II, which then activates transducin, a G-protein (guanine nucleotide-binding protein involved in second messenger cascades; a method of cellular signaling). Transducin then triggers the phototransduction cascade. The rhodopsin molecule remains inactive until its all-trans retinoid can be replaced by 11-cis retinal. The 11-cis isomer is necessary for the recombination with opsin, the portion broken away during photoisomerization. The all-trans retinoid is released from the opsin out of the cell to the retinal pigment epithelium or RPE (Bernstein, Law, & Rando, 1987). The RPE is the sheet of cells directly behind the neural retina, and functions as the layer where the all-trans retinoid converts back into its 11-cis isomer, which is then passed on to the photoreceptors. Lamb and Pugh (2004) have identified fifteen stages of the retinoid cycle, and diagrammed these stages accordingly (figure 2.3).

Figure 2.3. Taken from Lamb & Pugh, 2004. Schematic of the retinoid cycle; numbers indicate order of occurrence. Abbreviations are explained in the current text. The schematic is provided to show the reader the
complexity of the retinoid cycle. An overview of the cycle is provided in the current text. For a detailed review see Lamb & Pugh, 2004.


**Rhodopsin Regeneration**

When light hits the retina, the number of pigment molecules available for photon absorption is decreased. As the intensity of the light increases, the proportion of photopigment available for absorption is depleted monotonically (Hood & Finklestein, 1986). A reasonable assumption might be to suggest, then, that the decrease in available photopigment causes the decrease in visual sensitivity. If this were the case, a loss of 50% of the pigment molecules would double the threshold. The actual proportion of pigment molecules available to the system can be estimated (at equilibrium – that is, for long bleaching exposures) using the equation \( p = \frac{I_0}{I_0 + I_A} \), where \( p \) = pigment present, \( I_A \) = adapting intensity, and \( I_0 \) = a constant equivalent to 25,000 scotopic trolands (Rushton, 1956). This equation implies that the sensitivity in the rod system is affected very little by the loss of photopigment, except at very high light levels, much higher than those employed in this thesis. In fact, the rod system has reached saturation, and cones have taken over vision, well before even a small proportion of pigment molecules are depleted (Rushton, 1956); see figure 2.4.
Granit, Holmberg, and Zewi (1938) also suggested that light adaptation is not due to the depletion of photopigment molecules, but instead due to the presence of the products of light absorption. It has since been discovered that the rate of regeneration of visual pigment is directly proportional to the concentration of free opsin and 11-cis retinal.
Critically, the effect of bleaching leaves behind products, metarhodopsin and opsin, which mimic the effects of light, leading to the slow recovery of sensitivity during dark adaptation.

The current research aims to better understand visual sensitivity in the rod system. To follow is an explanation of the possible mechanism(s) for scotopic sensitivity regulation.
Chapter 3: The Mechanism for Scotopic Sensitivity Regulation

The scotopic region in which the rods operate initiates at absolute threshold in darkness and concludes somewhere above the photopic threshold. There are rod-cone interactions in the mesopic region. Vision that is well below the cone threshold is rod-driven, however. Sensory adaptation is one mechanism that allows the visual system to operate under such broad conditions. Adaptation, then, must decrease sensitivity to some lighting environments and increase sensitivity at others. When the light levels are bright, the visual system must decrease sensitivity such that the system does not saturate, but instead can detect local changes in light level (contrast detection). When light levels are dim, however, the system must increase sensitivity to be able to detect individual photons. How, then, is sensitivity regulated in the scotopic system specifically? As light intensity varies, to what can we attribute the increase or decrease in thresholds? Possible mechanisms of scotopic sensitivity regulation will be discussed in this chapter.

Hecht et al. (1942) believed that scotopic sensitivity in darkness was determined simply by the quantal fluctuations in the light source (photon noise). Light emitted from a source is Poisson distributed, meaning that the number of photons emitted by that light source varies randomly over time. How these quantal fluctuations affect our ability to detect photons of light is not certain, particularly when ambient light is present. The relationship between photon detection and photon noise can be estimated by fitting frequency of seeing curves with a cumulative Poisson distribution. If the number of quanta observed matches the average number of photons present, since the variance of a Poisson distribution is equal to its mean and photons are Poisson distributed, one can assume that
thresholds are governed only by the quantal fluctuation present in the light source. Hecht estimated a receptor absorption value of about 5-14 quanta, considering the number of photons incident at the cornea and the number of photons absorbed by the receptors. This estimation closely resembled the number predicted by a model in which dark light and photon noise together determine absolute thresholds (Sakitt, 1972).

As mentioned briefly in chapter 1, Rose (1942, 1948) and de Vries (1943, 1956) developed a theory of vision that related the eye to photoelectric cells or photographic plates, suggesting the limit of seeing set by the statistical fluctuations in the number of quanta absorbed. Rose did not, however take into account the different spectral sensitivities of the photoreceptors, used faulty measurements for the signal to noise ratio of the human eye, and assumed a constant temporal summation value across all conditions (Barlow, 1956). Likewise, de Vries validated his quantal fluctuation theory by assuming that thresholds are proportional to the square root of the background intensity without considering over what range that assumption was true. Barlow (1956) showed that this proportionality between the square root of the background and the threshold only holds under certain conditions, and postulated that large amounts of internal noise are critical in determining thresholds in both darkness and under very dim lighting levels.

Barlow (1956) suggested that not only does dark noise determine absolute threshold (thresholds measured in completed darkness), but it also determines thresholds over a range where the background noise contributes a negligible amount to the total noise. It is only after this point, when the TVI curve starts to turn upwards, that thresholds are proportional to the square root of the background, indicating thresholds determined by external noise; Weberian adaptation determines thresholds after the square root portion. If
Hecht et al., Rose, and de Vries were correct, and scotopic thresholds that comprise the flat portion of the TVI curve were mediated only by the external noise from the light source, then it must be concluded that the visual system contains very little internal noise. In other words, if thresholds are limited by photon noise alone, then the visual system must be quite ideal and virtually noiseless.

Rushton (1963, 1965) suggested that rod sensitivity regulation is controlled by an adaptation pool. Rushton claimed that prior to integrating into a neural pool, some type of linear summation of rod signals occurs over specific retinal regions. The combined average of these summations determines the factor to which the signal is attenuated by the adaptation pool (Rushton & Westheimer, 1962; Rushton, 1963, 1965). The attenuating factor is utilized to reduce sensitivity in the specific region subserved by the pool. Psychophysical evidence from a series of experiments using grating stimuli (MacLeod, Chen, & Crognale, 1989) also suggests that adaptation in the scotopic system is defined by an adaptation pool (about 10 min of arc in diameter) rather than the rods themselves.

Electrophysiological data in cats and monkeys suggest sensitivity regulation in the receptor. *In vitro* electroretinal stimulation of individual cat rods showed systematic light adaptation in rods, which developed over time (Tamura et al., 1989). Critically, they discovered negligible amounts of receptoral adaptation with light levels only slightly above absolute threshold, but as background levels increased the rods showed a progressive decrease in sensitivity allowing a 50-fold change in gain.

The amplification of single rod responses is accomplished, in part, due to convergence of many rods onto retinal ganglion cells (Sterling, Freed, & Smith, 1988). Rod signals are also amplified in other regions of the visual system. Animal research identifies
three pathways in which rod signals are transmitted, each preferring different light levels. Under dim lighting conditions the rod bipolar pathway is thought to be dominant. At higher light levels, signals undergo a rod-cone electrical coupling and/or the rod synapses to a class of OFF cone bipolar cells. Dunn and Rieke (2006) suggest that gain controls in the scotopic system, particularly at dim light levels, may be located between the rod bipolar cells and AII amacrine cells. Ultimately, it seems as though postreceptoral sites in the rod pathway are more important in terms of sensitivity regulation than the individual rods themselves.

In a 1999 review, Sharpe and Stockman discuss evidence from mouse, rat, cat, rabbit, and macaque identifying six different regions of rod-signal transmission that make up the three different rod pathways. The rod bipolar pathway consists of rod-rod bipolar metabotropic glutamatergic synapses, rod bipolar-amacrine AII cell glutamatergic synapses, amacrine II-ON cone bipolar electrical gap junctions, and amacrine II-OFF cone bipolar glycinergic synapses. The rod-cone gap-junction pathway transmits signals via rod-cone electrical gap junctions. The third OFF bipolar pathway transmits signals via inferred rod-OFF cone bipolar ionotropic glutamatergic synapses. Psychophysical and electrophysiological data from humans, along with data from a rod achromat and individuals with congenital stationary night blindness indicate at least two of these pathways in human observers. One pathway seems to be slow and more sensitive at low light levels, while the other, sensitive at higher light levels (entering the mesopic range), seems to be a faster pathway.

Physiological data from invertebrates and vertebrates indicate that the visual system has many sources of internal noise. Some data suggest that scotopic sensitivity
under dim light levels is regulated within the retina (*limulus*; Barlow, Birge, Kaplan, & Tallent, 1993, & *cat*; Tamura, Nakatani, & Yau, 1989). Aho et al. (1988) compared electrophysiological thresholds from the retinal ganglion cells of the cold-blooded *bufo bufo* toad with other animal species that have warmer body temperatures. They concluded that thermal isomerizations of rhodopsin in retina set the limits of vision; this conclusion, that heat determines dark noise, is supported by Barlow (1988). Differences between invertebrates, vertebrates, and primates could be attributed, then, to differences in thermal isomerization rates determined by the body temperature of the animal.

Schneeweis and Schnapf (2000) used electrophysiological techniques to better classify the contribution of receptor noise to sensitivity regulation. *In vitro* cell recordings from the macaque outer and inner segments were used to examine at least two types of noise located in receptors: long-term continuous noise and spontaneous isomerizations of rhodopsin. Specifically, they found that when voltage (which was in fact very noisy when all frequencies were considered) was filtered properly at the inner segment, the total dark noise corresponded to the much lower dark light estimates from human psychophysical studies. Additionally they found that when the intensity of a background was increased, the signal to noise ratio of single receptors followed square root behavior, the same behavior that is seen in TVI experiments with tiny, brief test spots. Schneeweis and Schnapf suggest that square root behavior in human detection experiments, then, could perhaps be explained by the signal to noise characteristic within single rods. Although these characteristics can be found in single rods, they must be located at a site beyond the outer segment (i.e., the inner segment or the terminal) after some type of noise filtering mechanism.
Stockman, Candler, and Sharpe (2010) argued that scotopic sensitivity is regulated postrecepto rally by changing the speed of the scotopic response. Stockman et al. studied the integration time of the scotopic system by measuring changes in phase delay as a function of adaptation level. Observers were first dark adapted for 40 minutes and, between trials, light adapted for 3 minutes. Rod isolation conditions were utilized. Stimuli, flickering lights, were presented separately to both eyes. Adaptation level was varied between eyes. When the phase or amplitude of the two stimuli did not match, interference occurred; if signals of opposite phases were presented to each eye, the resulting output was a flicker null. To identify temporal contrast sensitivity, subjects were told to adjust the contrast of the two signals until the flicker was at threshold. Results showed that temporal contrast sensitivity functions were dependent upon retinal illuminance level, reflecting the process of adaptation. More adaptation in the left eye caused observers to decrease the phase of the right stimulus, and vice-versa for a decrease in the adaptation level of the left eye. All observers showed correlated frequency-dependent changes in sensitivity, which the authors attributed to the shortening of the scotopic integration time with adaptation. Finally, because the light levels used were so dim, meaning the rate of photon absorption was extremely low, Stockman et al. suggest that receptoral sensitivity control was unlikely, indicating post-receptoral sites of scotopic temporal regulation.

In sum, much research has been done to better understand the mechanism of scotopic sensitivity regulation leading to a broad range of hypothesized contributing factors. Namely, a) photopigment depletion and regeneration, b) receptoral adaptation c) post-receptoral signal amplification, d) temporal integration differences in rod pathways, e) an adaptation pool, f) the statistical fluctuations in the number of quanta absorbed, g)
retinal adaptation, and h) the receptoral signal to noise ratio have been implicated in scotopic visual sensitivity regulation. The current research, a series of psychophysical experiments, will be used to understand the contributions of both external noise sources (photon-driven noise) and internal mechanisms (adaptation) to scotopic sensitivity regulation. The physiological location of adaptation is not tested here, but will be speculated upon in the General Discussion at the end of this thesis.

**Hypothesis**

The overall hypothesis to be tested in this thesis is that psychophysical sensitivity in the scotopic system in part reflects a rapid process driven by the statistics of photon noise, in addition to any fast (or slow) neural or receptoral adaptation processes. To predict thresholds, the basic equation that motivated the current research is presented below.

1. \( \text{constant} = \frac{\text{signal}}{\text{noise}} \)

Elaborated, each threshold measurement is based on the ratio of the signal (due to the test spot) to the noise. The noise is anything that will interfere with the system’s ability to detect the signal. Here, the numerator is a mean of correct detections and the denominator is the standard deviation of the noise. Assuming that the only sources of noise come from the background \( I \) and the dark light \( D \), substituting the proper variables implies equation 2:

2. \( \text{constant} = \frac{T^1}{\sqrt{I + D}} \), therefore \( T = \text{constant}(\sqrt{I + D}) \)

\[ \text{T is equivalent to the conventional } \Delta I \text{ used as the symbol for the signal. } T \text{ is used here to stand for threshold and will be used for the remainder of the paper.} \]
where \( T= \) mean threshold, \( I= \) background intensity, and \( D= \) dark light. \( I \) and \( D \) are each Poisson distributed, implying that both are mean and variance values which can be added because they are statistically independent. Let us now assume that the visual system uses a process of adaptation to determine thresholds. Equation 3 adds a term for that retinal gain, \( g \).

3. \( \text{constant}=g(\text{signal}/\text{noise}) \)

with the assumption being that adaptation due to the background changes the sensitivity to the signal by a factor of \( g<1 \). Therefore:

4. \( \text{signal}=(\text{constant} \times \text{noise})/g, \text{or } T=(\text{constant} \times \sqrt{I+D})/g \)

Using past literature (Barlow, 1956), we know that TVI curves for small spots follow the Square Root Law, and large test spots follow Weber's Law. The current research investigates the contribution of both photon-driven noise, which is always present, and \( g \) in threshold measurements under various lighting conditions. We predict the following values for \( g \):

5. \( g=\text{constant} \) (or 1)

for small spots, and,

6. \( g=1/\sqrt{I+D} \)

for large spots. Eq. (6) produces Weber law behavior. Empirical data (Barlow, 1956; discussed below) suggest to us that photon-driven noise limits threshold for small spots while both adaptation and photon-driven noise limit thresholds with large spots. Figure 3.1 shows the above predictions on a log/log scale to cover the broad range of light levels tested. The above predictions, then, suggest that both adaptation and photon noise follow
the Square Root Law, but inversely, such that Weber’s law is obtained when adaptation operates.

For $g$ to depend on spot size, it must be the case that small and large tests are detected by difference “channels” with different adaptational properties. Such “channels” correspond to receptive fields at the horizontal, amacrine, or ganglion cell level. Large receptive fields, suitable for detecting large spots, pool or summate background activity over a large area and need to decrease gain to prevent saturation (or at least delay it until stimuli are bright enough for cone vision). Small receptive fields pool or summate over a small region, and are thus less stimulated by the field, so need not decrease gain until much higher background levels are reached.

In summary, we suggest that photon noise from a background of intensity ($I$) will always drive up threshold in proportion to ($\sqrt{I}$), and a second gain-change stage will additionally reduce sensitivity to avoid saturating responses to large test spots in a manner also proportional to ($\sqrt{I}$), the combined effect giving rise to Weber’s law as $I = (\sqrt{I} \cdot \sqrt{I})$. To the extent that tiny dim tests will escape saturation, they will reveal the photon-driven noise effect alone. We suggest that this second gain-change stage can be thought of nominally as light adaptation, such that the system decreases its response to the large test after long-term exposure to a brighter background in order to avoid saturation of the system; this second stage allows rod vision to continue over a wider range of intensity.
Figure 3.1: Predictive graphs from equations 1-6 above: large (left), small (right); both log-log plots. The top (green) line follows Weber’s Law. The lower (orange) line follows the Square Root Law. The dotted line on the right corresponds to absolute threshold. For the large spot, we predict thresholds measured on the background will follow Weber’s Law, while thresholds measured just after the background is removed will follow the Square Root Law due to the removal of photon noise from the background. In the case of the small spot, on the right, we expect thresholds measured on the background to follow the Square Root Law, replicating the literature. Thresholds measured after the background has been removed should return to absolute threshold with the removal of photon noise from the background.
Chapter 4: General Methods

All viewing occurred through a traditional two-channel Maxwellian view optical system (Figure 4.1). A voltage-regulated 150 W xenon arc lamp (Osram XBO) in the optical system provides white light (LS), which passes through heat absorbing glass (HG) to remove infrared radiation. Some lenses were used as collimators to narrow the light beam (L12 & L22), while other lenses served as condensers, concentrating the light beam (L11, L20, L21, L10). Mirrors were in place to redirect any channels (M1 & M2). Maxwellian view optical systems are used, in part, so that variations in pupil size will not affect retinal illuminance. Accordingly, a 2mm hole was located at the first filament image of each channel (H1 & H2). Light from each channel is focused into a single spot at the plane of the subject’s pupil, resulting in a stable 2mm diameter image at the observer’s left eye.

Two variable neutral density wedges (mounted to computer controlled stepping motors) were placed near the images in channels 1 and 2 (W1, W2). A single step change is approximately 0.1 log units; steps in light intensity could be adjusted by either the computer or switches controlled by the observers (O). Channel one (red in figure 4.1) is the background channel. This channel provided a uniform field of light, which was used as a background on which the test was flashed; the intensity of this background could be varied in small steps during a session, while its color was fixed by interposing a narrow-band chromatic filter. Channel two (blue in figure 4.1) served as the test channel, and combined with the background channel at a beam splitter (BS3). A shutter (S) was used to present the flashed test spot.
Figure 4.1: Maxwellian view optical system depiction.

LS = Light Source
HG = Heat absorbing Glass
L = Lens
M = Mirror
MO = Monochromator
H = Hole
W = neutral density Wedge
CI = Channel 1 interference filter
BS = Beam Splitter
S = Shutter
ND = Neutral Density filter
FS = Field Stop
TS = Test Stop
ML = Maxwellian Lens
BF = Baffle
O = Observer

Red = Channel 1
Blue = Channel 2
Four 2’ arc diameter spots arranged in a diamond, appearing achromatic to the observer, were used to help observers attend to the correct location. A fifth spot was used as a fixation aid (Figure 4.2). Their intensity could be adjusted by the observer to keep them just at threshold as the background intensity increased. A field stop (FS) diameter of 22mm was used to define a background of 10 degrees nominally. Circular stops (TS) drilled in metal plates with beveled edges to reduce diffraction were selected to define test spots of 5’ arc or 1.3 deg diameter. Neutral density filters (ND1 & ND2) were used to vary the intensity of both the background and test channels. Beams of light were imaged upon a final Maxwellian lens (ML), and a baffle (BF) was used to prevent stray light from entering the eye. The head was positioned with the aid of a dental impression rigidly attached to a heavy milling device.

**Calibration**

Intensity was measured with a UDT photodetector head placed at a nodal point conjugate with the pupil. The head fed a custom-built amplifier. The sensitivity of the head to wavelength was provided by the manufacturer with a photometric ($V_\lambda$) filter attached in front of the collecting surface. The head and amplifier system were calibrated together by Charles Stromeyer of Harvard University. The calibration was checked against a second UDT head and manufacturer’s amplifier using the method of Westheimer (1966). The output of the amplifier varied by +/- 0.2 log units over the course of the study, introducing conservative small errors in the results. Light intensity was measured photometrically, and then converted into scotopic trolands. Measurements were made approximately bimonthly. Wedges and neutral density filters were calibrated *in situ* at the start of the experimental
series. Timing was checked with a photocell and counter-timer. Observers adjusted head position to ensure proper placement of the light on the pupil before every experiment across all subjects.
Figure 4.2: Maxwellian stimulus display schematic. The large circular patch is the adapting background. The blue dot in the center represents the test spot, which varied in size. The four central green dots indicate attentional aids. The green spot at the bottom of the background is the fixation aid. Background, test, and aids do not appear colored in experiments.

Subjects

Data were obtained from primary observers, namely, the author (BG) and the thesis advisor (AR), and one naïve undergraduate, RB. All subjects had normal or corrected to normal vision. BG and AR were the primary observers, thoroughly completing each experimental condition. Due to time limitations RB was not able to complete a significant amount of data collection in all experiments, but the experiments that were completed will be used as additional verification of the data from the primary observers. RB was
compensated with ten dollars per hour for all additional data collection after the completion of an independent study course.

**Procedure**

After 20 to 30 minutes of dark adaptation, thresholds were measured for a spot of light, a ‘test’. Subjects were exposed for 10 minutes to moderate room illumination of 28 cd/m\(^2\) on white paper, corresponding to 243 photopic trolands. Full recovery from this level is complete within 20 ms (Figure 2.2). The test was either 5’ arc (small) or 1.3 deg (large) in diameter. A 5’ arc test was chosen to reveal the Square Root law, as seen in the literature. For example, Sharpe et al. (1993) revealed the Square Root law using a small, 10’ arc test. Likewise, to replicate the literature, a 1.3 deg test was chosen to reveal the Weber law. The test spot was isolated to rods using eccentric fixation (5 deg), suitable wavelengths (500-530 nm), and dim backgrounds (480-530 nm). Fixation was at 5 deg below the test spot, not at 20 deg where rods are most numerous, to make report of the small test easier. Fixation at 5 deg was also convenient for comparison with the increment thresholds of Stiles (1939), which were obtained for a large, 200 ms test spot at this eccentricity. As a result, the rod portion of the TVI curve was somewhat reduced in range.

An adaptive up-down tracking method was used (Reeves, Wu, & Schrillo, 1998). The intensity of the test spot was initially random. The initial step size was 0.32 log units. If the observer reported a detection (“yes”), the test flash was dimmed. If the observer reported no detection (“no”), the test flash was intensified. Step size was doubled if the observer’s response were the same for three successive trials, and otherwise halved. Observers could press a no-judgment key (“I don’t know”) to keep the flash at the same intensity as the
previous trial. A trial terminated on reaching a step size of 0.02 log units, when the final value of the wedge was recorded. After 3-5 such values were collected, the computer calculated their mean and standard deviation; this mean was taken as the threshold. Generally, a dark adaptation period of 20-30 minutes, one block of absolute threshold measurements, and six blocks of experimental trials comprised one testing session. Each session lasted approximately 1.5-2 hours.

Test spots were presented for 200 ms and thresholds were collected in either
a) complete darkness (absolute threshold) (all experiments)
b) on a 10 deg in diameter adapting background (T_{on}) (Experiment 1 & Experiment 2)
c) just after the background had been turned off (T_{off}) (Experiment 1 & Experiment 2)
d) on a 10 deg in diameter flashed background (T'_{on}) (Experiment 3)
e) just after the background was flashed (T'_{off}) (Experiment 3)

Observers initiated each trial so as to be able to concentrate attention on the test location (5 deg outside the fovea) to maximum advantage. Participants required many hours of practice for thresholds to stabilize. Observers adapted to changes in the background between trials for 3 minutes, when applicable (Experiment 1). Some general information for each experiment is given below. See Chapters 5-7 for specific details regarding each experiment.

**Experiment 1**

Test flashes were presented for 200 ms in both on and off conditions (b & c). The gap between trials for on conditions was determined by the speed of the observer’s
responses (b). Observers adapted to the steady background for approximately 6000 ms between trials in the off conditions (c).

**Experiment 2**

Thresholds for a test flash were again measured on a background and after the background had been removed. This time, the gap between the background removal and test flash presentation varied between 200 ms-1600 ms (c).

**Experiment 3**

Observers measured thresholds on a flashed background and after a background had been flashed. The test stimulus and background flash duration for the off condition (e) was 200 ms. The on flash duration was 800 ms, such that 200 ms preceded the test spot, then the 200 ms test spot was presented, followed by 400 ms. No adaptation period was necessary between trials or blocks, as the background was black between each. The duration between the flashed background and the test spot (e) was 200ms.

**Curve-fitting**

A commercial program, Sigma Plot, was used to fit the dark light parameter in every data set, while the slope parameter was provided. Best fits were made by minimizing the least-squared error. The dark light estimate varied with slope, as the two values are not independent. The field point, defined as the field intensity that gives a threshold rise of 1 log unit, was determined by linear interpolation of the raw data, not the best fit curve (Table 8.1).
Chapter 5: Experiment 1, Replication of the Weber and Square Root Laws

Purpose
The aim of experiment one was two-fold; first, to replicate the Weber and Square Root Laws for rods using both small and large test spots by measuring thresholds on a steady background of increasing intensity, and second, to measure thresholds for both spots after turning off the background to estimate the effects of removing photon noise from the background.

Procedure
Experiment 1 utilized the general methods explained in Chapter 4. Specifically, thresholds were measured for a spot of light (either 5’ arc or 1.3 degrees) on a ten degree diameter adapting background ($T_{on}$) and just after the background had been turned off ($T_{off}$) (see Figure 5.1 for a basic schematic of the experimental procedure). The intensity of the background increased incrementally over 6 blocks by a value of .30 log units. Between blocks, observers adapted to the background intensity of the upcoming block of trials. $T_{off}$ was measured either 400 ms or 600 ms after background offset. It should be noted that a separate experiment (Experiment 2 presented in Chapter 6) measured increment thresholds at a variety of SOAs (200 ms-1200 ms). Test spots were presented for 200 ms in $T_{on}$ and $T_{off}$ conditions. Test parameters were chosen to facilitate comparison with Stiles’ data (1939). Data from Stiles is displayed below in Figure 5.2 for comparison.
Figure 5.1. Experiment 1. The table below displays the progression of one block over time and the first portion of the next block. Column one below shows a schematic of the stimuli. Column two shows the profile of the stimulus. Column three shows a textual description of each piece of the experiment. After 20-30 minutes of dark adaptation, absolute thresholds were measured. Observers then adapted to the background intensity for the upcoming block for 3 minutes. The first half of each of six blocks measured thresholds on lit background ($T_{on}$); the second half of the block measured thresholds 400 or 600 ms after the steady lit background was removed ($T_{off}$). On each trial in $T_{off}$, the background turned off 200, 400, or 600 ms before the test flash (the ‘gap’ duration), and then returned 400 ms after the test flash, remaining on for 6 sec to top up any adaptation before the next trial commenced.

<table>
<thead>
<tr>
<th>Experiment 1</th>
<th>Stimulus</th>
<th>Profile</th>
<th>Description</th>
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<td>Background Adaptation</td>
</tr>
</tbody>
</table>
Figure 5.2. Data from Stiles (1939). Used to facilitate comparison based on similarity of parameters: 5 deg parafoveal fixation, adapting background of 500 nm, and 1 deg test spot.

Variation of log (threshold) with log (field intensity) for a 1° flashing test stimulus of yellow light (exposure time 0.063 sec.) on a blue-green field: 5°-parafoveal vision. (Stiles, 1939)
**Results**

Figures 5.3 and 5.4 show data for the two primary observers, BG and AR, and one naïve observer, RB, at two test sizes, 1.3 deg and 5’, respectively. The number of thresholds averaged into each data point is given in table 8.1.

Cone thresholds were measured for AR and BG using the same procedures as those used for Experiment 1, however only 3 minutes of dark adaptation were employed along with central fixation. The cone plateau is noted on the y-axis of each graph.

Error bars correspond to the standard error of the mean between experiment sessions. Data points lacking error bars come from one session only. Any threshold measured with a large standard deviation within trials was repeated, thus wide error bars mostly reflect between-session variability. All data were measured in log scotopic trolands and plotted accordingly.

At the start of each experimental session, absolute thresholds were measured. The absolute threshold value was subtracted from $T_{on}$ and $T_{off}$ values, on a session-by-session basis, to normalize the data for between session variability. The horizontal axis corresponds to the log scotopic troland value of the adapting background. The vertical axis gives the threshold, relative to the absolute threshold, in log units, for $T_{on}$ and $T_{off}$. The zero point on the vertical axis refers to the value of the absolute threshold, because when $T_{on}=\text{Abs}$, it follows that $\log(T_{on}/\text{Abs})=\log(1)=0$. Defining sensitivity as the inverse of threshold, as is usual practice in psychophysics, $\log(\text{sensitivity})=-\log(\text{threshold})$, any increase in threshold due to the presence of the background represents an equal decrease of sensitivity on a log scale. Closed symbols show $T_{on}$ and open symbols, $T_{off}$. A dashed line is used to display the predicted $T_{on}$ curve, and a dotted line is used to display the predicted
The lateral position of both curves being set by the best-fit dark light value (see above).
Results: large test spot

Figure 5.3: Filled symbols (T_{on}) and open symbols (T_{off}) are thresholds plotted relative to absolute threshold (0.0). The dashed line shows the predicted T_{on} values using a Weber fit for the 1.3 deg test (slope of 1). The dotted curve shows the predicted T_{off} values with a slope of 0.5. The test size, test wavelength, background wavelength, gap duration (T_{off}) and proportion of variance accounted for (T_{on}), and the dark light value (in log units) are located in each figure below.

AR: 1.3 deg, 530 nm test
480 nm background, 600 ms gap
\( \hat{r}^2(T_{on})=0.93, \log(D)=-3.04 \)
BG: 1.3 deg, 530 nm test
480 nm background, 400 ms gap
$R^2(T_{on})=0.97, \log(D)=-3.26$
RB: 1.3 deg, 500 nm test
480 nm background, 600 ms gap
$\tau(T_{on}) = 0.95$, log(D) = -2.72
**Discussion: large spot**

The increment threshold curve ($T_{on}$; filled symbols) has the expected Weber slope (1.0) for all large spot (1.3 deg) data across subjects, as predicted. The thresholds measured 400 or 600 ms after background offset ($T_{off}$; open symbols) fall below the increment thresholds, as expected at the start of dark adaptation. When the $T_{on}$ curve has a slope of 1.0, the $T_{off}$ thresholds drop half-way to absolute threshold at all background intensities. This effect can be explained by the removal of photon-driven noise ($I$; $I=$background intensity) when the background is turned off. Again, photon-driven noise is distributed as a compound Poisson; hence the variance is reduced in proportion to $I$ (Krauskopf & Reeves, 1980). Turning off a background of intensity $I$ removes photon noise so thresholds fall at the very start of dark adaptation in proportion to Square Root($I$). This is so whether increment thresholds obey the de Vries-Rose law or the Weber law.
**Results: small test spot**

Figure 5.4: Filled symbols ($T_{on}$) and open symbols ($T_{off}$) are thresholds plotted relative to absolute threshold (0.0). The dashed line shows the predicted $T_{on}$ values using the Square Root Law fit (slope of 0.5); the dotted curve shows the predicted $T_{off}$ values with a slope of 0.0. For BG’s data below, both Weber and square root fits are displayed for both sets of small spot data below (discussion to follow). Data for BG 500 nm test, 530 nm background, were subjected to 2-point smoothing due to increased variability. The test size, test wavelength, background wavelength, gap duration ($T_{off}$), proportion of variance accounted for ($T_{on}$), and dark light (in log units) are located in each figure below.
AR: 5' test, 530 nm test
480 nm background, 600 ms gap
$r^2(T_{on})=0.98$, log(D) = -3.39
AR: 5', 500 nm test
530 nm background, 600 ms gap
$r^2(T_{on}) = 0.97, \log(D) = -3.2$
BG: 5', 500 nm test
480 nm background, 200 ms gap
\( r^2(T_{on}) = 0.77 \) (Sqr Root Law), \( \log(D) = -3.89 \)
BG: 5', 500 nm test
480 nm background, 200 ms gap
$r^2(T_{on})=0.96$ (Weber), log(D) = -2.86
BG: 5', 500nm test
530 nm background, 600 ms gap
$r^2(T_{on})=0.83$ (Sqr. Root Law), log(D) = -3.69

log threshold

log scotopic trolands

cones
BG: 5', 500nm test
530 nm background, 600 ms gap
$\hat{\sigma}(T_{on}) = 0.96$ (Weber), $\log(D) = -2.7$
RB: 5', 500 nm test
480 nm background, 200 ms gap
$r^2(T_{on})=0.90$, $\log(D)=-3.54$
RB: 5', 500 nm test
400 nm background, 600 ms gap
$r^2(T_{on})=0.92$, log(D) = -3.56
**Discussion: small test spot**

The tiny spot experiments yielded the predicted 0.5 slope in most cases. For observer AR, when the $T_{on}$ curve had a slope of 0.5, and the background was about -1.7 log scotopic trolands or less, the $T_{off}$ thresholds dropped to approximately the long-term absolute threshold. An exception to this pattern occurred after exposure to backgrounds higher than -1.3 log scotopic trolands, where thresholds did not fall as far as predicted. The duration of the gap seemed to affect AR's thresholds slightly, such that $T_{off}$ thresholds did not drop *completely* to absolute threshold with gap durations of 200 ms. When the gap was 600 ms, AR's thresholds fully recovered to zero, the absolute threshold. Observer RB's increment thresholds also showed square root behavior (slope reaching 0.5) when the test was presented on backgrounds of -1.3 log scotopic trolands or less. When the gap was 600 ms, RB's $T_{off}$ thresholds dropped back to absolute threshold, consistent with AR's. When the gap was 200 ms, RB's $T_{off}$ thresholds drop to absolute threshold only for backgrounds less than or equal to about -2.5 log scotopic trolands.

The TVI curves for observer BG did not replicate the 0.5 slope often cited in the literature (Barlow, 1956), but instead showed a near-Weberian slope. Data from Sharpe et al. (1993) also suggest that not all observers show precise square root behavior for tiny spots; some of their observers had slopes greater than 0.5 (see appendix A for these data). $T_{off}$ thresholds dropped from the near Weber slope to a slope of 0.5 when the gap duration was 600 ms, replicating results for the large test spot. $T_{off}$ for BG dropped from the near Weberian slope back to absolute threshold when the gap duration was 200 ms.
Conclusion

It is unclear why the rod TVI curves differ for small and large spots in some situations, whereas the cone TVI curves do not (Reeves, Wu, Schirillo, 1998). According to Rushton (1963, 1965), dim backgrounds light-adapt a neural pool and not the rods themselves. We theorize that to the extent that small receptive fields that detect the small tests do not benefit from pooling, the increment thresholds ($T_{on}$) for these spots should follow the de Vries-Rose law, and do so up to a background level of about 3 scotopic trolands (0.48 log scotopic trolands) when the receptors themselves begin to light-adapt according to Weber’s law. The larger receptive fields that detect the large spots do benefit from pooling, but this pool is light-adapted by the background, thus raising $T_{on}$ from the de Vries-Rose law to Weber’s law. In both cases, removing the background removes photon noise but, momentarily at least, leaves the state of adaptation (gain) unchanged, so that the ratio $T_{on}/T_{off}$ is proportional to $\sqrt{I}$. This account explains the results for observers AR and RB except for the 5’ arc $T_{off}$ thresholds for backgrounds of over -1.7 log sc. td for gap durations of 600 ms. Because the 200 ms gap duration produced thresholds that either did not completely drop to absolute threshold, or only dropped for dim backgrounds, the effect of gap duration was investigated more in Experiment 2.

It is unclear why BG shows Weberian slopes for both the 1.3 deg test spot and the 5’ arc test spot increment thresholds. We theorize that the test spot is being detected by large receptive fields in both cases, rather than stimulating tiny receptors for 5’ arc test spots. If the 5’ arc tests were being detected by tiny receptive fields, the noise from the background would be less influential on thresholds. It seems as though large receptive fields instead of tiny ones are being stimulated by the tiny test spot, causing a greater loss in sensitivity as
the system is trying to overcome the effect of noise from the background. If this explanation is true, it still does not account for the drop back to absolute threshold with 200 ms gaps.

The variable effect of the gap duration on the $T_{off}$ measurements will be addressed in experiment 2.
Chapter 6: Experiment 2, Stimulus Offset Timing

Purpose

In experiment two the delay time from field offset to test presentation was varied. Delays longer than the integration period should have no effect on threshold if photon-noise abolition is the only factor involved. If long-term adaptation only was responsible for the increase in thresholds, longer stimulus offset delays would be required for sensitivity to fully recover. Several delay times were tested to determine if this was the case. All delays were equal to or longer than the integration time of the scotopic pathway, about 200 ms. Results from experiment 1 suggest that the gap duration does affect thresholds. Perhaps the amount of light adaptation present in the system does need gap durations slightly longer than 200 ms for the effects of photon noise removal to appear.

Procedure

Experiment 2 utilized similar methods to those described in Chapter 4. Specifically, thresholds were measured for a spot of light (either 5’ arc or 1.3 degrees) on a ten degree diameter adapting background (T_{on}) and just after the background had been turned off (T_{off}) (see Figure 6.1 for a basic schematic of the experimental procedure). The intensity of the background was held constant throughout the duration of the experiment. The delay between stimulus offset and test presentation was incrementally increased for each block of trials. Observers started each session by measuring absolute thresholds. Ideally, T_{on} should not be affected by the test offset delay manipulation, as T_{on} was measured on a background of constant intensity to which the observer was re-adapted for 6 sec between trials. However, increasing SOA implied longer and longer periods in the dark, which might
have altered the state of adaptation and thus T_on. To check that T_on was in fact stable, it was re-measured after each new SOA.

T_off was measured either 200, 400, 600, 800, 1000, 1200, or 1600 ms after background offset. The photon-noise abolition hypothesis predicts that Stimulus Offset Asynchrony (SOA) will have no effect on the T_off for the tiny spot (which will already be at absolute threshold), and will not affect the T_off for the large test spot until SOA is so long that the second gain change begins to increase the sensitivity of the pool. The time constant on this latter process is probably on the order of minutes, given the slow course of dark adaptation recorded with large test spots (Hecht, Haig, & Chase, 1937), and so would not be expected to affect thresholds for the first second or so after the background was turned off. When possible, more than one background intensity was used between sessions to ensure that results could be generalized across a wider variety of light levels.²

² It should be noted that due to technical problems with the equipment, a limited number of data were collected for Experiment 2. Ideally, we would have collected data with dim, moderate, and bright backgrounds using each of the seven gap durations for all observers with both test sizes.
Figure 6.1: The table below displays the progression of Experiment 2 over time. Column one below shows a schematic of the stimuli. Column two shows the profile of the stimulus. Column three shows a textual description of each piece of the experiment. After 20-30 minutes of dark adaptation, absolute thresholds were measured. Observers then adapted to the background intensity used for the remainder of the experiment for 3 minutes. The first half of each of six blocks measured thresholds on background; the second half of the block measured thresholds 200, 400, 600, 800, 1000, 1200, or 1600 ms after the steady background was removed. The first half of each block was not part of the experimental manipulation, but was simply measured to ensure that thresholds remained stable throughout the duration of the experiment. The background was presented for 800ms before incremental gap duration increases. Unlike experiment 1, there was no background adaption period between blocks, as the entire experiment was conducted with the same background intensity.
**Results**

Figures 6.2 shows large test spot data for observers BG and RB. Figure 6.4 shows small spot data for observers AR and BG. Most sessions were repeated and thresholds were averaged. Each individual threshold was measured according to the procedure described in Chapter 4: General Methods.

As in figures for Experiment 1, error bars correspond to the standard error of the mean between experimental sessions. Data points lacking error bars come from one session only. Any threshold measured with a large standard deviation within trials was repeated, thus wide error bars mostly reflect between-session variability. The absolute threshold value was subtracted from $T_{on}$ and $T_{off}$ values to normalize the data for between-session variability. The horizontal axis corresponds to duration of the gap between the offset of the background and the onset of the test in milliseconds. The vertical axis corresponds to the threshold in log units, relative to absolute threshold, for $T_{on}$ and $T_{off}$. Closed symbols show $T_{on}$ and open symbols, $T_{off}$. $T_{on}$ was measured as a control for stability. Only the data presented for $T_{off}$ were potentially affected by the experimental manipulation.
Results: large test spot

Figure 6.2: Experiment 2 (SOA), large spot (1.3 deg). Filled symbols ($T_{on}$) and open symbols ($T_{off}$) are thresholds plotted relative to absolute threshold (0.0). The test size, test wavelength, background wavelength, and background intensity is located in each graph below. The horizontal axis refers to the gap duration in milliseconds between the offset of the background and the test presentation (SOA). The vertical axis refers to the threshold in log units.

BG SOA: 1.3 deg, 500 nm test
480 nm, dim background
BG SOA: 1.3 deg, 500 nm test
480 nm, moderate background
BG SQA: 1.3 deg, 500 nm test
480 nm, bright background

log threshold vs gap in ms
RB SOA: 1.3 deg, 500 nm test
480 nm, dim background
**Discussion: large test spot**

For observers BG and RB thresholds were relatively consistent between trials for the control (\(T_{\text{on}}\)) conditions. As the background light increased, so did the variability between blocks for \(T_{\text{off}}\) values. Specifically for both observers, the drop in thresholds remained consistent for all gap durations when the background was dim. \(T_{\text{off}}\) values for moderate backgrounds for BG were higher with shorter gap durations (200ms), but seemed to recover and remain stable after the gap durations reached about 400 ms. When the background was bright, BG needed at least 600 ms gap durations for \(T_{\text{off}}\) thresholds to recover.
Results: small test spot

Figure 6.3: Experiment 2, small spot (5’ arc). Filled symbols are T_{on} data. Filled symbols (T_{on}) and open symbols (T_{off}) are thresholds plotted relative to absolute threshold (0.0). The test size, test wavelength, background wavelength, and background are located in each figure below. The horizontal axis refers to the gap duration in milliseconds between the offset of the background and the test presentation (SOA). The vertical axis refers to thresholds in log units.
AR SOA: 5', 500 nm test
530 nm, moderate background
BG SOA: 5', 500 nm test
530 nm, dim background
**Discussion: small test spot**

For observers AR and BG thresholds were relatively consistent between trials for the control ($T_{on}$) conditions. With moderate backgrounds, AR needed longer gap durations (at least 600 ms) for $T_{off}$ thresholds to recover back to near absolute threshold. With dim backgrounds, AR’s thresholds recovered back to absolute threshold and remained stable after 200 ms; BG seemed to recover back to absolute threshold quickly (200 ms gap duration) but thresholds began to rise with longer gap durations.

**Conclusion**

Results from experiment 2 suggest that at least a portion of the drop in threshold seen when the background is removed (experiment 1) is due to light adaptation, in that scotopic sensitivity has not yet fully recovered back to absolute threshold with bright backgrounds and short gap durations. In some cases, the increment thresholds continue to rise on a slope of 0.5 (small spot), when the extinction ($T_{off}$) threshold rises above the absolute threshold, even at 600 ms (Experiment 1: Figure 5.4), a result that is not explained by the theory. Some subjects show continued drop in extinction thresholds from 200 ms out to 600 ms in the dark. The stimulus durations used here were fixed at 200 ms and gap durations were set to be 200-1600 msec. If the period of summation was always less than 200 ms, and if the theory is true, then the drop should be complete within 200 ms. Either the summation lasts longer for these subjects, or other processes (such as the formation of after-images) get in the way, or the theory is too simple.

With small spots, Observer BG recovered quickly, after 200 ms, but then thresholds began to rise when gap durations reach 400 ms. Perhaps these results can be explained by
a criterion shift that occurs between 200 and 600 ms gap durations. If observer BG uses the background offset as an attentional cue to detect the small test spot, then test spots presented closer in time to the offset would be easier to detect. After 600 ms in the dark, however, the observer may have a harder time allocating his/her attention to the proper location. If in 600 ms the eyes or attention wanders a fraction of a degree away from the location of the test spot, detection of the tiny spot would suffer (as in figure 6.3: BG) whereas detection of the large spot (fig 6.2 BG) would not.
Chapter 7: Experiment 3, Flashed Background

**Purpose**

Rather than adapting to a *steady* background (Experiment 1), a background with incrementally increasing intensities and a test spot were *flashed* simultaneously to determine how threshold varies due to photon noise rather than effects of long-term light adaptation. The theory predicts that small test spots will produce increment curves that follow the Square Root Law, given that light adaptation is not contributing due to the brief duration of the background. Thresholds measured after the flashed background should fall back to absolute threshold (slope of 0.0), due to lack of photon noise present during test presentation. Increment thresholds for large spots may also follow the Square Root Law, if light adaptation of the pool takes time, in which case, extinction thresholds should again fall to absolute threshold; however, if pool adaptation is very rapid, the increment thresholds will again follow the Weber Law and the extinction thresholds the Square Root Law.

**Procedure**

After 20-30 minutes of dark adaptation, thresholds were measured for a spot of light with the background turned off (absolute threshold) and on a briefly flashed background (symbolized by a prime, as $T'_{on}$). There was no light adaptation between trials. Similar to the $T_{off}$ condition in experiment one, thresholds were also measured 200ms after the flashed background was extinguished (symbolized $T'_{off}$). The test spot was isolated to rods using eccentric fixation (5 deg), suitable wavelengths (500 nm), and short-wavelength
backgrounds (480 nm). Both small (5’arc) and large (1.3 degree) test spots were used. Test spots were presented for 200 ms.

Due to limitations of the equipment, $T’_{on}$ and $T’_{off}$ thresholds were measured using different experimental sessions, unlike in Experiment 1. Rather than presenting the test on the lit background for the first half of the blocks, these experiments measured thresholds without the lit background at the beginning of each block; during the second half of each block, the test spot was presented either with the simultaneously flashed background ($T’_{on}$) or 200ms after ($T’_{off}$). This method, although more time consuming, allowed us to repeatedly make absolute threshold measurements between blocks since there was no lit background. By measuring the absolute threshold between each block we were able to check for consistency in each observer’s absolute threshold and to confirm that there was no long-term adaptation affecting absolute threshold due to the flashed background. In fact, we found that absolute thresholds did not vary over time (data not plotted). Results for the $T’_{on}$ and $T’_{off}$ trials, which came from different sessions, will be displayed on the same graphs. Figure 7.1 is a schematic depiction of the experimental conditions.
Figure 7.1: Experiment 3. The table below displays the progression of experiment 3. Column one shows a schematic of the stimulus. Column two shows the profile of the stimulus. Column three shows a textual description of each piece of the experiment. The first row displays the absolute threshold measurement, which was taken at the beginning of every session. $T_{on}$ and $T_{off}$ conditions were run in different experimental sessions. Thus, the middle two rows show the $T_{on}$ sessions, and the last two rows show the $T_{off}$ sessions. The first half of each block in both types of session measured thresholds without a background as a control. For the $T_{on}$ sessions, the second half of the block measured thresholds of a test presented on a briefly flashed (200 ms) incrementally lit background. For the $T_{off}$ sessions, the lit background was flashed for 200 ms, then the test spot was presented after a 200 ms gap.
Results

Figures 7.3 and 7.4 show data for the two primary observers, BG and AR, and a naïve observer, RB. The number of sessions averaged into each threshold is provided in figure 8.1. Each individual threshold was measured according to the procedure described in Chapter 4: General Methods.

Similar to Experiments 1 and 2, error bars correspond to the standard error of the mean between experimental sessions. Data points lacking error bars come from one session only. Any threshold measured with a large standard deviation within trials was repeated, thus wide error bars mostly reflect between-session variability. The horizontal axis corresponds to the log scotopic troland value of the flashed background. The vertical axis corresponds to $T'_{\text{on}}$ (closed symbols) and $T'_{\text{off}}$ (open symbols), relative to the absolute threshold.
Results: large test spot

Figure 7.3. Experiment 3, large spot (1.3 deg). Filled symbols ($T'_{on}$) and open symbols ($T'_{off}$) are thresholds plotted relative to absolute threshold (0.0). The dashed line shows the predicted $T'_{on}$ values using a Weber fit for the 1.3 deg test (slope of 1), the dotted curve shows the predicted $T'_{off}$ values with a slope of 0.5. The test size, test wavelength, background wavelength, background duration, gap duration ($T'_{off}$), proportion of variance accounted for $T'_{on}$, and dark light (in log units) is located in each figure below.

- BG: 1.3 deg, 500 nm test
- 480 nm, 200 ms flashed background ($T'_{off}$)
- 200 ms gap
- $r^2(T'_{on}) = 0.92, \log(D) = -2.42$
RB: 1.3 deg, 500 nm test
480 nm, 200 ms flashed background (T'_{off})
200 ms gap
r^2(T'_{on})=0.84, log(D)= -2.49
Discussion: large test spot

T' on curves for observers BG and RB followed the Weber Law, implying a slope of approximately 1.0. T' off curves seem to recover back to absolute threshold for BG, and almost all the way back to absolute threshold for RB. Extinction curves start to turn up around -1.0 log scotopic trolands for both observers.
Results: small test spot

Figure 7.4: Experiment 3, small spot (5’ arc). Filled symbols (T’\text{on}) and open symbols (T’\text{off}) are thresholds plotted relative to absolute threshold (0.0). The dashed line shows the predicted T’\text{on} values using a Square Root Law fit (slope of 0.5); the dotted curve shows the predicted T’\text{off} values with a slope of 0.0. The test size, test wavelength, background wavelength, background duration, gap duration (T’\text{off}), proportion of variance accounted for (T’\text{on}), and dark light (in log units) is located in each figure below.

AR: 5’, 500 nm test
480 nm, 200 ms flashed background (T’\text{off})
200 ms gap
r^2(T’\text{on})=0.88, log(D)= -2.81
BG: 5', 500 nm test
480 nm, 200 ms flashed background (T'\text{off})
200 ms gap
\hat{r}^2(T'_{\text{on}})=0.79, \log(D) = -4.04
RB: 5', 600 nm test
480 nm, 200 ms flashed background ($T'_{\text{on}}$)
200 ms gap
$r^2(T'_{\text{on}})$ = 0.76, log(D) = -3.53
Discussion: small test spot

Threshold increment curves for AR, BG, and RB seemed to follow the Square Root Law fairly well ($r^2=0.88, 0.79, 0.76$). The extinction curves tended to drop back to absolute threshold, albeit not so precisely for AR and RB. For AR, the $T'_\text{off}$ data seem to increase slightly as the background intensity increases. BG’s $T'_\text{off}$ data quickly recover back to absolute threshold and remain on a slope of 0.0 regardless of the background intensity. Observer RB’s extinction data had more variability than AR and RB, but it seems as though her thresholds hovered somewhere around absolute threshold except for her small spot thresholds, which curiously did not recover well after extinguishing dim fields.

Conclusion

Results from experiment 3 suggest that for the large spot, increment thresholds behave the same way for a briefly presented background and a steady background (Experiment 1), generally compatible with the results of Adelson (1982) who found only a slight difference between these conditions (for fields less that 1 scotoic troland). In contrast, thresholds on flashed fields rise markedly if the field and test come on simultaneously, as is frequently done, e.g., Geisler (1979), but we regard this as an outcome of Crawford masking rather than of the light adaptation studied here. Our result implies that a briefly flashed background does produce the combined effects of photon noise and light adaptation on detection of a test, that is, an increment curve with a slope of approximately 1.0.

The $T'_\text{off}$ data however differ from the $T'_\text{off}$ results found in Experiment 1. With both test spot sizes, the extinction curves follow a slope of approximately 0.0, implying complete
recovery to absolute threshold. These results suggest that once the photon noise has been removed, the lingering effects of the 200 ms background are not strong enough to continue to elevate thresholds. The light adaptation seen in the increment threshold must be a short-term effect, as a long-term effect would still have continued to raise extinction thresholds for the large spot.

In some cases, the extinction curves did not recover completely to zero (Figure 7.4 AR & RB). These results could be explained by the gap duration between the flashed test and the flashed background. Results from Experiment 2 suggested that AR and RB needed at least 600 ms to completely recover back to absolute threshold. Even though the background was flashed rather than steady (as in Experiment 1 & 2), it seemed to have the same effect on the increment curve. These results would imply that AR and RB still needed 600 ms to recover after seeing the background, regardless of its duration. Observer BG seemed to prefer the 200 ms gap for tiny spots (Experiment 2). Accordingly, BG’s T’_off data recovered back to absolute threshold for the small spot. This was also true for BG’s large spot data.

Interestingly, observer BG suggested that detecting the spot after the background had been flashed was significantly easier for this experiment than the others. Perceptually, BG claimed that after the background had been briefly flashed, the test spot seemed to be obviously distinct for both test sizes, as opposed to Experiment 1, during which the test seemed like more of a white/gray blur. At threshold, the large spot to looked similar in both Experiments 1 and 3, but the small spot looked more vivid in Experiment 3 than Experiment 1. The difference between the appearance in T’_on and T_on (small spot) suggests different mechanisms, perhaps a difference in the size of the receptive field detecting the
test between experiments. Note: for BG the slope for the increment thresholds in Experiment 1 was best fit at 1.0, whereas in Experiment 3, a 0.5 fit was preferable.
Chapter 8: GENERAL DISCUSSION

The aim of the current research was to collect data investigating the roles of photon-noise and adaptation on scotopic thresholds. I suggest that photon noise contributes not only to absolute thresholds, as shown by Hecht et al. (1937), but also contributes to increment thresholds. The current data provides evidence for at least two components of scotopic sensitivity regulation: first at low light levels, thresholds for the small test spot are determined by photon noise, and second, at brighter light levels and for large spots, thresholds are determined by photon noise and light adaptation.

Background light

The effect of light adaptation is to de-sensitize the scotopic pathway, raising thresholds. This occurs when each receptor receives more than a few photons per second from the background- a level we call 'intense' to distinguish it from dim and moderate backgrounds that do not light adapt the rods themselves. Dim backgrounds, though clearly visible, have little to no effect on threshold. Moderate backgrounds desensitize in proportion to their intensity, so a simple multiplicative factor, the 'gain', is enough to describe the effect of light adaptation. Gain is 1.0 in the dark, but brighter backgrounds reduce gain. The reduction in gain helps protect the rod pathway from saturation, allowing it to continue functioning over a broad range of light levels before the cones are activated. On intense backgrounds, however, the scotopic pathway does saturate; a non-linear effect that cannot be described just by 'gain'. Excluding these intense backgrounds, any light adaptation revealed by increases in threshold is likely to be due to adaptation of the post-receptoral pathway, the rod-bipolar synapse or higher-level synapses in the retina, not
adaptation of the receptors themselves (which is currently thought to occur above 3 scotopic trolands).

**Photon noise**

Not only does the lit background change the state of adaptation, but it is also a source of random variations, called photon noise. This variation is Poisson distributed or proportional to mean light level. Averaging both spatially and temporally reduces variation in proportion to the number of independent samples taken in the average. Averaging therefore reduces noise, but to deliver useful vision, the rod system must still maintain temporal and spatial acuity; averaging is therefore limited. In fact the system averages perfectly over about amount of 100 ms (the critical duration) and a few degrees of visual angle (the critical area). The critical area, but probably not the critical duration, decrease as the light level increases (Sharpe et al., 1993) and more photons are available to permit higher acuity.

For tiny test spots and dim backgrounds (e.g. Figure 5.4 for AR 500 nm test, 530 nm field, at background intensities up to about -1.3 log scotopic trolands), the situation is simple; gain is 1.0. This is because so few photons are caught by the minute receptive fields needed to see the tiny spot, that there is no threat of saturation. Therefore, the increment threshold is determined solely by the photon noise in the lit background, hence the slope of 0.5. The extinction threshold (that is, $T_{off}$) equals the absolute threshold, because there is no background to provide photon noise, and gain remains 1.0, hence the slope of approximately 0.0. For tiny spots and bright backgrounds (e.g. Figure 5.4 for AR 500 nm test, 530 nm field, at background intensities beyond -1.3 log scotopic trolands), the
increment threshold rises above 0.5 indicating that some light adaptation is occurring and gain is less than 1.0. In these cases, the extinction threshold should drop, but not as far as the absolute threshold, just as far as is determined by $\sqrt{I}$ (i.e., losing the photon noise by keeping the gain effects).

For large spots and dim to moderate backgrounds (Figure 5.3), the situation is complicated by the need to protect the system from saturation. The large receptive fields that detect large spots receive many photons from the background endangering saturation, so their gain must be reduced. Threshold data show that the light adaptation of the scotopic system with large spots proceeds with a slope approximately 1.0. To obtain a (log) slope of about 1.0, the gain term must account for a slope of approximately 0.5, given that photon noise accounts for a slope of 0.5, and the two effects, noise and gain, multiply. Turning off the background removes the photon noise without (by assumption) permitting any change of gain to occur, because gain only recovers slowly, as shown by classic data on scotopic dark adaptation. So $T_{on} / T_{off}$ is again determined by $\sqrt{I}$. The extinction threshold should have a slope of 0.5. For large spots on intense backgrounds, cones take over the increment threshold, but rods still determine the extinction thresholds, which should continue on a slope of 0.5. Data from experiment 1 of the current research confirm this pattern of predictions.

Experiment 3, which used a flashed background rather than a steady one, provided slightly different results. Although the increment thresholds for the large spots did not follow the Square Root Law prediction, the large spot extinction thresholds did follow the predictions (an almost full recovery back to absolute threshold), as did all 5’ arc data. It seems as though light adaptation is a very quick process (200 ms) when the stimulus is
large enough, and that its effects are somewhat related to the duration of the light presentation causing the adaptation. In other words, it seems as though gain is not so slow to recover when the light that induced the gain was presented for durations equivalent to twice the critical duration.

**Physiology**

Light adaptation has been established in the receptors, the rods themselves, for brighter backgrounds, those delivering more than a few quanta per sec per rod. Any such adaptation must raise the threshold for all test spots, large and tiny, on a slope of more than 0.5. The current research did not employ such bright backgrounds. However, using Aguilar and Stiles’ method to investigate psychophysical thresholds in the region of rod saturation, it would be possible to determine if $T_{on}/T_{off}$ obeyed the $\sqrt{I}$ law even in these cases. Dark adaptation of the rods following exposure to such brighter backgrounds involves a complex and slow regeneration process. In contrast, the drop in threshold following extinction of dimmer backgrounds does not involve this form of slow recovery process, and according to the current research, appears to be completed in 200-600 ms.

**Dark Light**

If it is assumed that the dark light value is an intrinsic property of the retina then it should remain stable across test spot sizes and should be approximately the same for all normal observers. To find out if this was true, best-fit dark light values, obtained from each observer in each experiment, were compared for consistency across conditions for steady and flashed background TVI curves and across subjects. An average dark light was calculated and the best fit program was rerun for each experiment. Although these values
were remarkably consistent for the steady experiment across subjects (log(D)= -3.39, -3.58, and -3.54) for the small spot, and relatively consistent for the large spot (log (D)= -2.93, -3.26, and -2.68), fitting the curves with an average log (D) for all experiments resulted in worse fits (proportion of variance accounted decreased by 0.15 on average) than leaving this as a free parameter (precise D, log(D) and r² values are presented in table 8.1). We can assume from these data that the dark light value was variable based on the condition of the experiment and thus is not an fixed property of the human visual system.

The dark light values for the small test spot were on average about 0.5 log scotopic trolands below the values for the large test spot. By introducing the concept of the minimal observation area (MOA) this shift of 0.5 log units can be explained. The MOA is not the same as Ricco’s area, which is the area of summation of test area (Ricco, 1877), but instead is the area to which observers can restrict their attention during test detection; the MOA is the area in which one gathers noise. This shift of 0.5 log units might occur if the minimal observation area (MOA) was 0.42 sq. deg., corresponding to a test diameter of 0.73 deg. The observation area for the large spot would be equal to the physical area of the large spot, but would be 0.42 sq. deg for the tiny spot, larger than its physical area of 0.001 sq. deg. Observers would, therefore, collect more noise from the background when observing the large spot than the tiny spot, in the ratio of (1.30/0.73)²=3.26, or -0.51 log units.

This explanation may be useful for interpreting test results for observer BG with the small test spot. It seems as though the amount of noise in the MOA is large enough to activate large receptive fields, resulting in Weberian slopes rather than square root slopes, as seen by the other observers and often cited in the literature. When the background is flashed, rather than steady, however, the MOA is affected by the temporal properties of the
stimulus; the visual system has less time to sum the noise.

Limitations

The choice of spot sizes (5' and 1.3 deg) was determined more by convenience and by the literature, than by any precise theoretical motivations. However, different components of the visual system need to integrate over different regions locally to detect lines, points, edges, and so on, versus large uniform expanses (tree trunks, grass) and these spots may tap into such different components, as we assumed when relating to receptive field size. The psychophysical measure of critical area using spots cannot explain scotopic spatial vision beyond a very simple characterization of the initial input, and entirely ignores configural effects (Sakitt, 1971).

The equipment used to collect data was also a limiting factor. In some occasions, there was a light leak problem resulting from the field shutter. When the light leak was noticed, the subjects were trained to re-position the shutter. However, this was tricky and lead to some poor quality extinction thresholds for the naïve observer RB (see page 91). To be able to run experiment 3, an additional circuit was added to the optical system which allowed for the test spot to be displayed after the flashed background. The additional circuit limited the gap duration to 200 ms or less. Ideally, longer gap durations would have been tested and compared to Experiment 1.

In general, rod experiments are difficult because they require a long period of dark adaptation, practiced observers to manipulate the equipment in the dark, and precise controls to ensure that there is no light leakage in the testing room. Consequently, these experiments are limited in terms of the number of subjects that can participate in the
experiment; the current research cannot make use of the psychology department subject pool. We present here an incomplete design due to time limitations. Ideally, we would have all three subjects complete the same amount of sessions for each experiment. One additional observers has been added and will be included in a potential future manuscript. In addition both within-session and between-session variability is larger than for similar experiments performed on the cones, in part because the need to use eccentric rather than foveal stimuli makes attending to the test spots more difficult, even despite the array of fixation aids. However, the data were reliable enough for our main conclusions to stand.

**Conclusions**

Turning off the background removes photon-driven noise and permits thresholds to drop in turn. Visual sensitivity is determined by three factors: intrinsic noise (dark light), photon noise, and receptoral and post-receptoral adaptation. By scaling thresholds to the absolute threshold and by measuring both increment and extinction thresholds, for comparison with each other, we have been able to isolate the photon noise contribution to the rod-mediated threshold. It is considerable, not just at absolute threshold (as was known by Hecht et al., 1942), but on dim and moderately lit backgrounds. This conclusion for the rods is in agreement with that reached by Krauskopf and Reeves (1980) for the cones; despite the very different properties of the two pathways, both share the same requirement, to see details (such as small spots) on uniformly-lit backgrounds.

At all but the dimmest levels, uniform backgrounds appear uniform to the observer; they do not seem to twinkle, despite the random nature of light. A uniform percept is the result of averaging photon noise over space and time in order to reduce the effects of the
noise. Such averaging inevitably smears out photons from the test spot, and therefore raises test spot thresholds. This is in addition to any increase of threshold due to physiological changes in gain consequent on the mean light level. Identifying sensitivity with the inverse of the increment threshold as is commonly done blurs this distinction, since increment thresholds reflect both photon noise (for tiny spots, almost exclusively so) and the state of adaptation.

An alternative, and common, hypothesis is that photon noise plays little or no role in the increment threshold but only at absolute threshold. Since photon noise must increase with background level, the only way to overcome it is to average it out. As the light level increases, the extent of averaging must increase, to keep up with the increase in the noise. Averaging can be increased by increasing the critical area and/or the critical duration. However, because both either stay about the same or decrease with light level (Sharpe, 1993), it seems that this alternative is ruled out.

Future research will compare psychophysical data collected from the current experiments with physiological data (e.g., Lamb & Pugh, 2004). We anticipate that, if the photon-noise hypothesis holds up for rod increment thresholds, there will be evidence in the physiological literature for Poisson or Poisson-like statistics in rod-driven responses, over a corresponding range of background intensities. There appears to be some such evidence for salamander rods (Nakatani & Yau, 1988) and toad rods (Rieke & Baylor, 1996), but evidence from primate rods is quite limited (but see Schneeweis and Schnapf, 2000).

In the future, we hope to expand the current research to more subjects to further investigate individual differences between subjects, such as the Weberian adaptation with
tiny test spots exhibited by one subject compared to square root behavior exhibited by the
the other two observers. Some data has already been collected for another subject. Thus
far, her data suggest the same basic pattern of results for the large spot and small spot as
observers AR and RB here. More data is necessary to make any definitive conclusions;
however, we suggest here that photon-driven noise in the receptors and early stages of the
scotopic pathway, plays an important part in controlling thresholds not only in total
darkness but also in conditions of dim illumination.
Table 8.1: Tabular summary of each experiment for each subject. D=Dark Light, $r^2$=proportion of variance accounted for by the predictive fit for $T_{on}$. $r^2$ (mean D)=proportion of variance accounted for if we substitute the average D into the best fit equation. Dim & bright # = number of sessions run for the dim data points (usually the first 6 points on each graph) and the number of session run for bright data points (usually the last 6 points on each graph), respectively. * = from Sharpe et al., 1993.

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References


Appendix A

Data from Sharpe et al. (1993). The current experiment utilized a small spot stimulus that was similar to the stimuli presented in Figure C below. These data suggest that slopes for small spots do not always replicate the Square Root law.
Appendix B

Mean log D for the current data (large and small spots +/- 1 standard error) and data from 2 normal observers from Sharpe et al (1993).